OSTEOLOGY AND RELATIONSHIPS OF THE ROOSTERFISH, *NEMATISTIUS PECTORALIS* GILL[1]

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Abstract: The status of the roosterfish, *Nematistius pectoralis*, long has been in doubt. It alternatively has been considered a member of the Carangidae or to represent a monotypic family. An investigation of the osteology of *N. pectoralis* indicates that it should not be placed in the Carangidae, but merits separate familial status. *N. pectoralis* differs from members of the Carangidae in that the gas-bladder enters the skull through large foramina in the basioccipital and contacts the inner ear, the three anal spines are normally arranged, and the interosseus space of the shoulder girdle is well developed. The two families are similar, however, in most other skeletal features and are regarded as closely related.

Patterson's suggestion that the Carangidae have been derived independently from the Beryciformes is not supported. His primary indicator of relationships, caudal rays with forked bases that clasp the hypurals, has been developed independently in a number of unrelated lineages. Other resemblances between the Cretaceous berycoid genus *Aipichthys* and modern carangids are regarded as products of convergent evolution.

INTRODUCTION

Nematistius pectoralis, the roosterfish or papagallo, is a large, fast swimming, predaceous fish of the eastern tropical Pacific (Fig. 1). The most striking external feature of the species is the presence of elongate, free dorsal spines, which account for the generic and vernacular names.

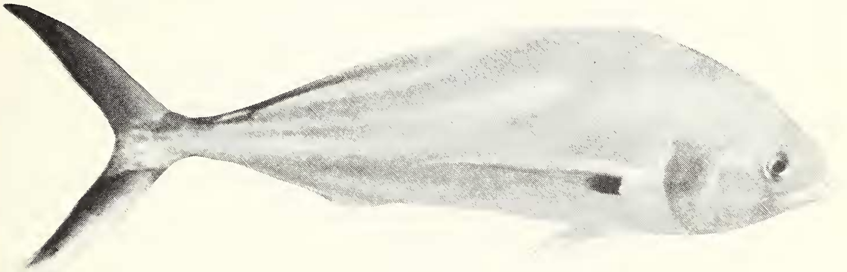

Figure 1. *N. pectoralis*, a living adult. In normal swimming the elongated dorsal spines are folded down. (Photograph by E. M. Hobson.)

The familial placement of *Nematistius* fairly can be termed an ichthyological football. It variously has been regarded as a member of the Carangidae (Boulenger 1910; Regan 1913; Greenwood et al 1966) or placed in a separate family (Gill 1864; Jordan and Evermann 1898; Berg 1947; Freihofer 1963). It will be noted that some of the most distinguished names in the history of ichthyology are ranged on either side of the question.

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Considering the unfavorable ratio of ichthyologists to fishes, it is perhaps not surprising that no one has attempted to settle the matter by an investigation of the internal anatomy of *Nematistius pectoralis*. Starks (1908) briefly described the connection between the inner ear and the gas bladder (otophysic connection, vide Greenwood et al 1966); Berg (1947) pointed out its possible taxonomic significance; and Freihofer (1963) indicated that the ramus lateralis accessorius nerve conformed to his Pattern 10, in distinction to the Carangidae, but that is all. An investigation of the osteology of *Nematistius* is made more meaningful by the recent publication of extensive descriptions of the osteology of a number of carangid genera and species (Suzuki 1962).

MATERIALS AND METHODS

Dried, partly disarticulated preparations as well as stained and cleared specimens were used. Details of the gas-bladder connection with the inner ear were worked out by dissecting specimens in which the gas-bladder had been filled with latex. In the following material list (S) refers to a stained specimen, and (D) to a dried preparation. The material used in this study is housed in the collections of the Scripps Institution of Oceanography (SIO), Biology Department, University of California, Los Angeles (UCLA) and the National Marine Fishery Service, Southwest Fisheries Center, La Jolla (BCF).

Nematistiidae-*Nematistius pectoralis:*SIO62-22, entire skeleton of an 886 mm (fork length) adult (D); SIO unnumbered, head and appendicular skeleton of an adult (D); UCLA S402, two neurocrania and vertebral columns (D); UCLA A-225 3 (32-79.5) (S); UCLA W53-297, 1 (17.5) (S).

Carangidae-*Caranx melampygus,* BCF422-26 (S); *Chloroscombrus chrysurus* BCF422-19 (S); *Decapterus* sp. SIO unnumbered (D); *Gnathanodon speciosus* BCF 422-17 (S); *Hemicaranx zelotes* BCF422-6 (S); *Selene oerstedi* BCF422-2 (S); *S. vomer* BCF422-22 (S); *Seriola dorsalis* SIO unnumbered (D); *S. mazatlana* SIO 57-16 (D); *Trachinotus carolinus* BCF422-5 (S); *T. falcatus* BCF422-21 (S); *T. goodei* BCF422-23 (S); *Vomer declivifrons* BCF422-11 (S); *V. setapinnis* BCF422-9, BCF422-20 (S).

Scombridae-*Sarda chiliensis,* SIO unnumbered (D); *Scomber japonicus,* SIO unnumbered (D); *Thunnus obesus,* SIO unnumbered (D).

Coryphaenidae-*Coryphaena hippurus* SIO54-160 (D).

Engraulididae-*Anchoa* sp. SIO unnumbered (S).

Stromateidae-*Peprilus* sp. SIO unnumbered (S).

Serranidae-*Mycteroperca jordani* SIO62-706 (D).

Kyphosidae-*Girella nigricans* SIO unnumbered (D); *Medialuna californiensis* SIO unnumbered (D).

OSTEOLOGY

Neurocranium.—(Figs. 2, 3). Bones of neurocranium relatively dense, except for cancellous areas along anterodistal margin of supraoccipital, dorsolateral portions of lateral ethmoids, and ventrolateral margins of frontals.

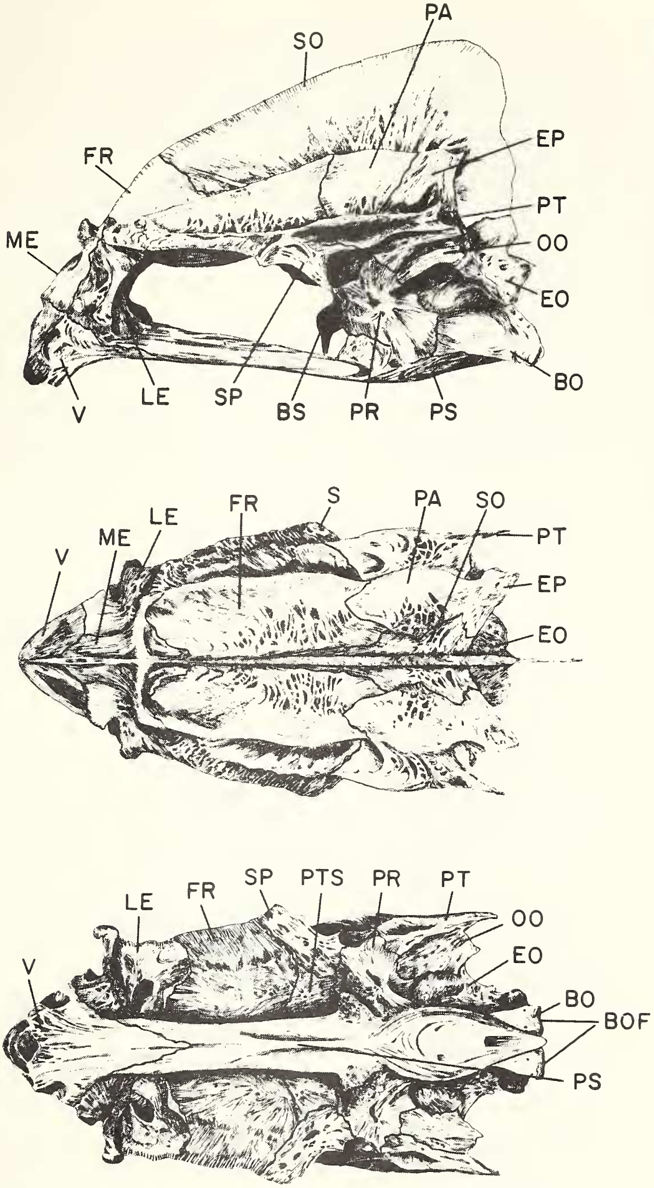

Figure 2. *N. pectoralis,* neurocranium. A—side view, B—top view, C—bottom view. Abbreviations: BO, basioccipital; BOF, basioccipital foramen; BS, basisphenoid; EO, exoccipital; EP, epiotic; FM, foramen magnum; FR, frontal; LE, lateral ethmoid; ME, mesethmoid; OO, opisthotic; PA, parietal; PR, prootic; PS, parasphenoid; PSF, parasphenoid foramen; PT, pterotic; PTS, pterosphenoid; SO, supraoccipital; SP, sphenotic; V, vomer (prevomer).

Neurocranium deep, and relatively broad anteriorly; its outline subrectangular when viewed from above. The most prominent features are the lateral crests and median crest. The ventralmost crest is formed by the pterotic and frontal, the next by the epiotic, parietal and frontal, and the medial crest by the supraoccipital, frontals, and, to a minor extent, mesethmoid.

Mesethmoid roughly cruciform in anterior view, with dorsal ridges on the lateral arms and a pronounced median ridge that continues downward onto anterior face of vomer (prevomer). Vomer deep, with a relatively short shaft. Tooth patch ovoid. Lateral ethmoids with large openings for olfactory tracts. Nasals ligamentously attached to ethmoids.

Roof of orbital cavity formed mainly by frontals, pterosphenoids and sphenotics. Anterior opening of braincase bounded by pterosphenoids and basisphenoid. Pterosphenoids not meeting across midline, but with medial processes posteriorly, which almost come in contact. Basisphenoid in contact with pterosphenoids and prootic dorsally and parasphenoid ventrally. Myodome large and deep.

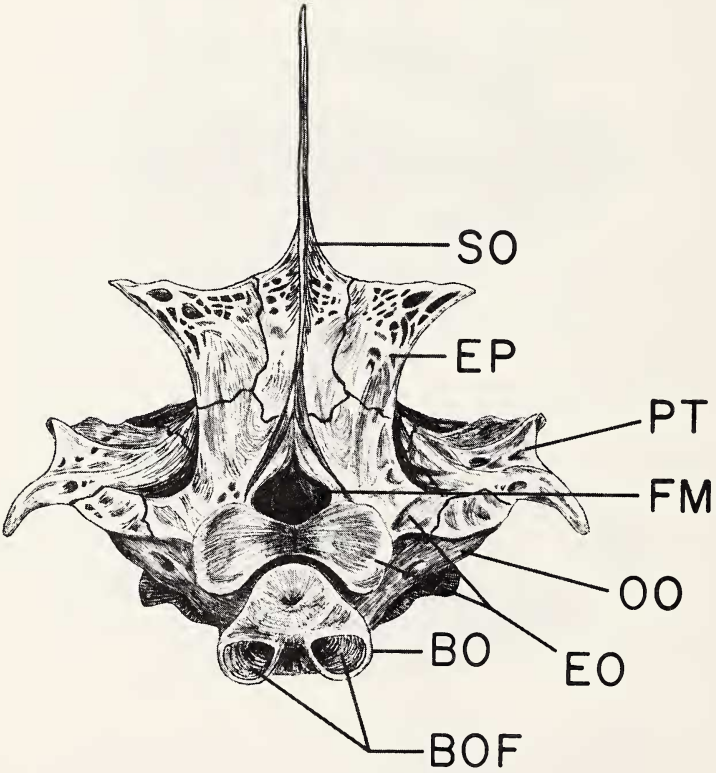

Figure 3. Neurocranium of *N. pectoralis*, rear view. Abbreviations as in figure 2.

Parasphenoid with a sharp keel to just behind level of orbital cavity, then expanded laterally and flattened. Parasphenoid in contact with vomer and lateral ethmoids anteriorly, and with prootic and basioccipital posteriorly. Posterior opening of myodome developed as a large canal bounded dorsolaterally by basioccipital and ventrolaterally by parasphenoid. Basioccipital contacting prootic anteriorly, parasphenoid ventrally, first vertebra posteriorly, and exoccipitals anteriorly.

On either side of basisphenoid, beneath and lateral to condyle, are two canals with posterior openings that lead into the auditory bulla. Each canal receives a process from the gas-bladder. These anterior processes of the gas-bladder extend forward to the region of the inner ear, but do not come in contact with it. Our observations thus confirm those of Starks (1908). The exoccipitals, bounded by the supraoccipital, epiotics, pterotics, opisthotics, prootics and basioccipital, are in contact along the midline, above and below the foramen magnum.

Opisthotic almost excluded from top of skull by the overlying pterotic and exoccipital. Pterotic with a strong backward projection, and a long socket which receives one facet of head of hyomandibular. At junction of the pterotic, epiotic and parietal there is an unossified area bridged by cartilage.

Prootic forming a major part of the posterolateral wall of the neurocranium. At its anterodorsal corner it, together with the sphenotic, forms a deep socket for an articular facet of the hyomandibular. Pars jugalis with but two openings, thus agreeing with other perciforms (Patterson 1964:434-438).

Supraoccipital with a high crest, which extends far forward over frontals, and posteriorly to exoccipital. Superficially frontals in contact for only a short distance; they are separated by the supraoccipital posteriorly and the mesethmoid anteriorly.

The general shape of the jaws is indicated in figure 4. The maxilla fits closely into the groove on the dorsolateral surface of the premaxilla and is braced anteriorly against the palatine. Supramaxilla rather loosely attached to maxilla. Premaxilla with two ascending processes anteriorly and a lower one posteriorly. The ascending (anteriormost) process contacts the mesethmoid and the posterior ones contact the maxilla. The premaxilla is very similar to those illustrated by Suzuki (1962) for various carangid genera. The lower jaw is of normal perciform type, except that the angular (retroarticular) is fused to the articular (angular).

Suspensorium.—(Fig. 5). Suspensorium and opercular bones well integrated. Posterolateral face of hyomandibular deeply grooved to receive ascending process of preopercle. Palatine with a narrow band of teeth.

Symplectic firmly joined to quadrate and metaptergyoid, and metapterygoid further united with hyomandibular and, on its inner face, with ectopterygoid.

Hyoid Apparatus.—(Fig. 6). Ceratohyal and epihyal firmly united by deep sutures on medial face. A well-developed, elongate-oval foramen in ceratohyal, from which a groove runs anteriorly and posteriorly along its lateral face. Posteriorly, this groove continues onto epihyal, forming a deep excavation. There are seven branchiostegals, three articulating with the inner face of the ceratohyal, two with its outer face, and two with the outer face of the epihyal.

Orbital Bones.—(Fig. 7). Six suborbital bones, including dermosphenotic (only the first four are figured). Lachrymal without the outward curvature described by

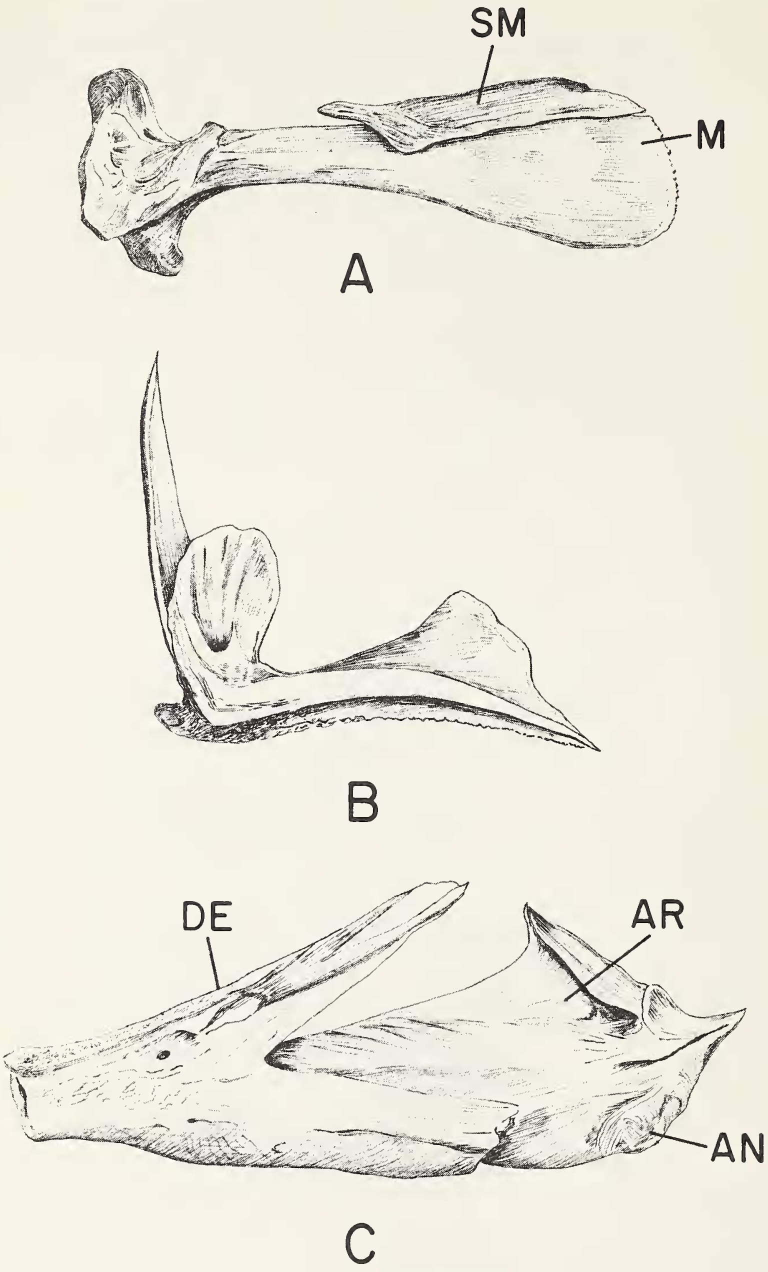

Figure 4. Jaws of *N. pectoralis*. A—maxilla and supramaxilla; B—premaxilla; C—lower jaw. Abbreviations: AN, angular (articular); AR, articular (retroarticular); DE, dentary.

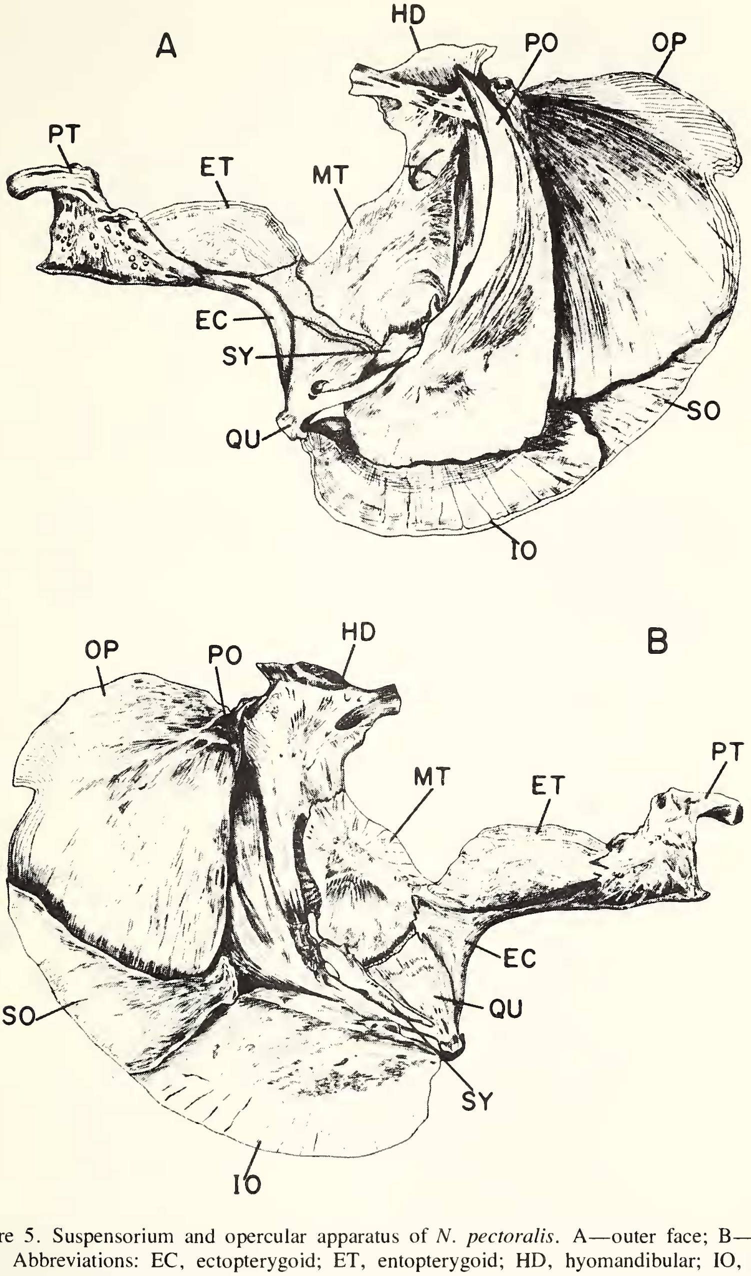

Figure 5. Suspensorium and opercular apparatus of *N. pectoralis*. A—outer face; B—inner face. Abbreviations: EC, ectopterygoid; ET, entopterygoid; HD, hyomandibular; IO, interopercle; MT, metapterygoid; OP, opercle; PO, preoperacle; PT, palatine; QU, quadrate; SO, subopercle; SY, sympletic.

Suzuki (1962) for many carangids, but anterior notch characteristic of the Carangidae weakly developed. Second suborbital trapezoidal and overlapping first, so that it contacts its outer face rather than its posterior edge for most of its length. Third circumorbital a thin, curved, inward directed lamina articulating with second along its upper inner border. Third suborbital forming major part of suborbital ring, in this respect agreeing with such carangid genera as *Elagatis* and *Naucrates*.

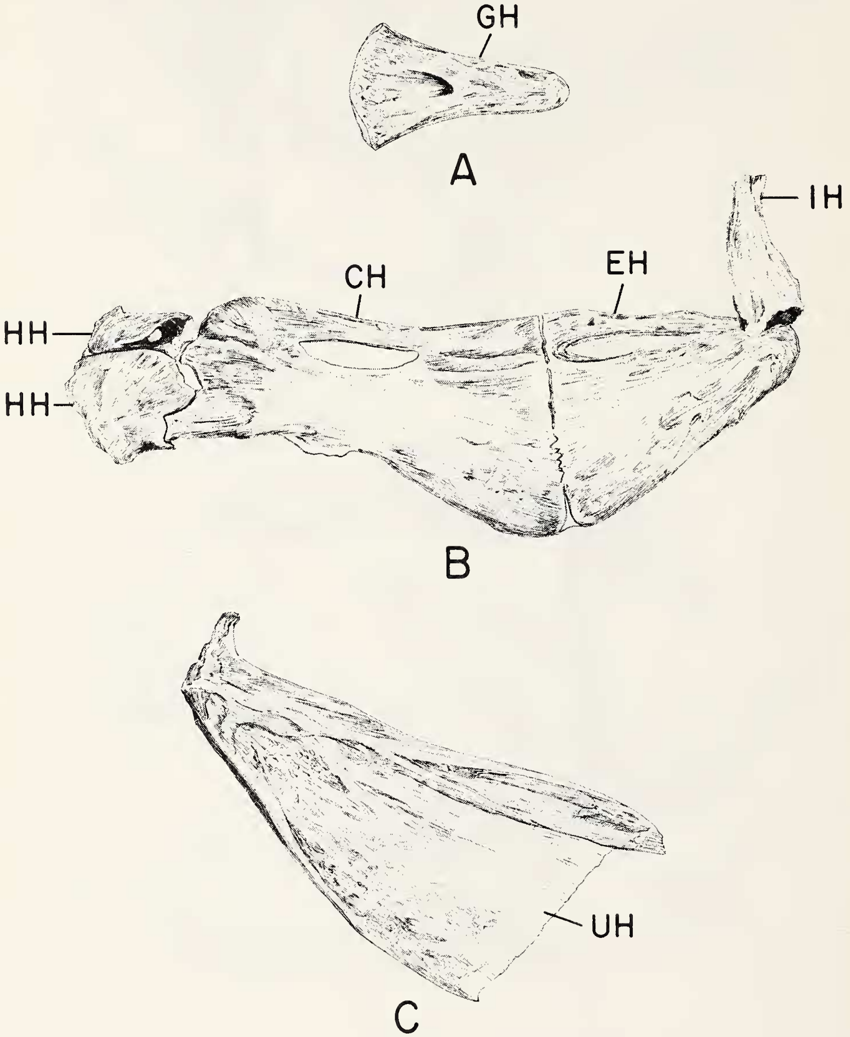

Figure 6. Hyoid apparatus of *N. pectoralis*. A—glassohyal, dorsal view. B—paired elements of hyoid arch. C—urohyal. Abbreviations: CH, ceratohyal; EH, epihyal; GH, glossohyal; HH, hypohyals; IH, interhyal; UH, urohyal.

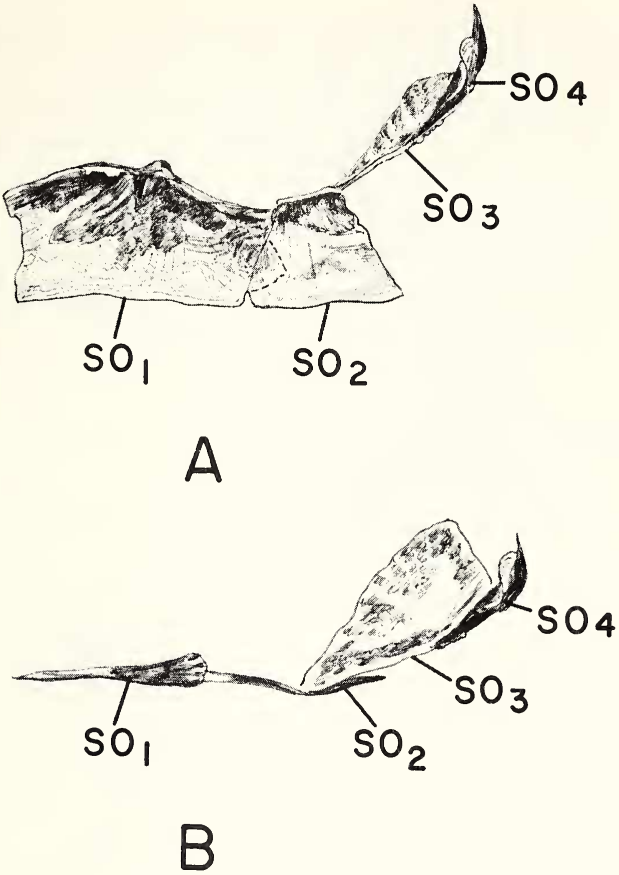

Figure 7. Orbital bones of *N. pectoralis,* SO_5 and dermosphenotic not shown. A—lateral view. B—top view.

Limb Girdles.—(Figs. 8, 9). Scapula with two foramina. Anteriorly is the normal perciform foramen. In *Nematistius,* the cleithrum forms part of the anterior border of this foramen on its lateral surface; medially the foramen is completely within the scapula. Behind this foramen is a second smaller one, which is absent in the Carangidae, as in all of the perciforms illustrated or described by Starks (1930) except *Cirrhites rivulatus* and *Scorpaenichthys marmoratus.*

All four actinosts borne on scapula. First short and hourglass shaped; remainder more elongate.

The pelvic girdle bears a striking resemblance to those illustrated by Suzuki (1962, Fig. 45). Pelvic plate thin and flattened and with lateral keel. Two sharp keels ventrally (subpelvic and interpelvic keels of Suzuki). Ischial processes long and curved.

Vertebral Column.—There are 10 precaudal and 14 caudal vertebrae, including the urostylar centrum. Articular facet of first vertebra for basioccipital condyle facing down and slightly forward, at an angle of approximately 45° to the axis of the body. Articular surfaces for exoccipital condyles facing almost straight forward. First neural arch autogenous. Second centrum about half as long as first and two thirds as long as third. First two neural spines curve forward and are in close contact. They appear fused in some specimens.

First epipleural rib articulating with first neural arch, second with second centrum, and remaining 5 are borne on pleural ribs. Pleural ribs eight; the first is associated with third vertebra. First three ribs sessile, remainder borne on

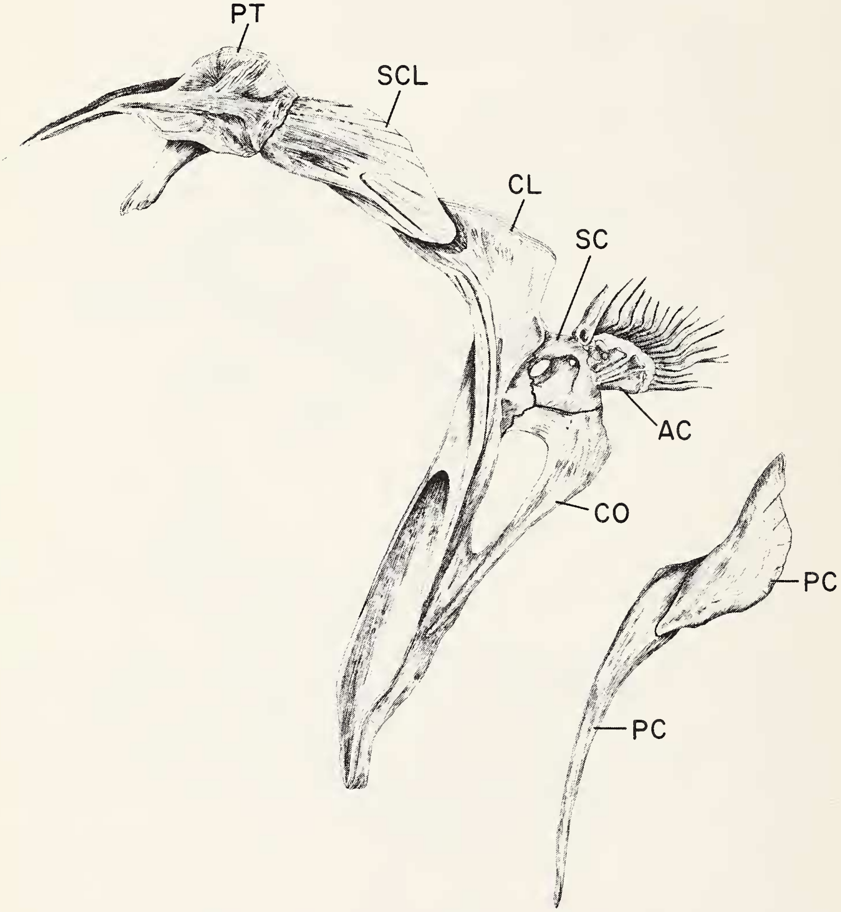

Figure 8. Pectoral girdle of *N. pectoralis*. Abbreviations: AC, actinosts; CL, cleithrum; CO, coracoid; PC, post-cleithra; PT, post-temporal; SC, scapula; SCL, supracleithrum.

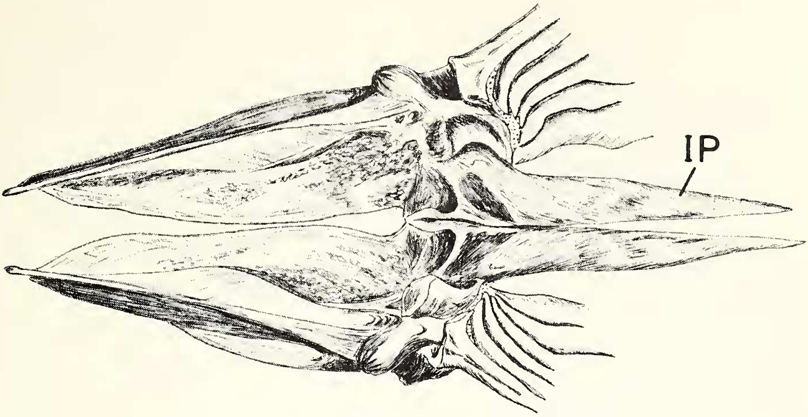

Figure 9. Pelvic girdles of *N. pectoralis*. IP, ischial process.

parapophyses. First vertebra with parapophyses is the fourth, first with a haemal arch the eighth. Inferior foramina of Starks (1911) lacking in parapophyses and haemal arches.

Ventral zygapophyses do not strongly interlock. Dorsal zygapophyses interlock strongly anteriorly, but become opposed by 17th vertebra.

Neural and haemal spines posterior to the 19th vertebra sloping strongly backward, increasing the rigidity of caudal peduncle.

Caudal Skeleton.—(Figs. 10, 11). Principal caudal rays 9 + 8. Caudal rays, except for middle two, cleft at the base and broadly overlapping skeletal supporting elements. Procurrent caudal rays borne by neural spine of antepenultimate vertebra and haemal spines of last two preural vertebrae. Two specimens with 10 procurrent rays above and 9 below, one with 9 and 8.

Elements associated with ural centrum forming a compact unit. Individual elements are difficult to distinguish in dried preparations, and more easily discerned in stained and cleared juveniles (contrast figures 10 and 11). Hypurals reduced by fusion to four. Upper and lower enlarged hypural plates each represent the fusion of two hypurals. In small juveniles there is a foramen in the lower expanded hypural plate, but this becomes obliterated with growth.

Dorsal and Anal Fins.—(Figs. 12, 13). Three median bones in advance of dorsal fin. We follow the terminology of Smith and Bailey (1961) who termed these structures predorsal bones. The first interneural element is an enlarged structure that bears two spines. The arrangement of three ray-less elements, followed by one which bears two rays is 0 -0 -0 -2 in the shorthand terminology of Smith and Bailey. For reasons given in the discussion, we regard the expanded element in *Nematistius* as representing the fusion of the first pterygiophore with the proximal and medial radials of the second pterygiophore. The first three anal spines are closely approximated, rather than unequally spaced as in the Carangidae, nor is the first anal pterygiophore as stout and expanded ventrally. However, the structure

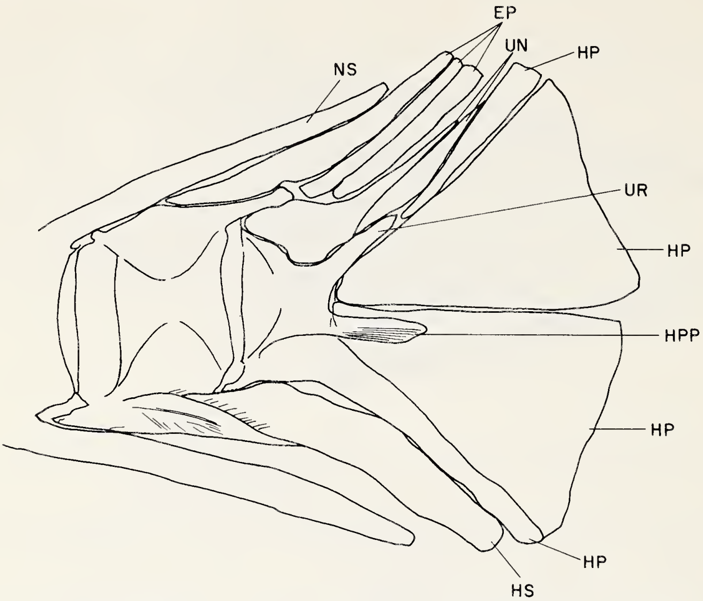

Figure 10. Caudal skeleton of a large juvenile *N. pectoralis* (dried preparation). Abbreviations: EP, epural; HP, hypural; HPP, hypurapophysis; HS, haemal spine; NS, neural spine; UN, uroneural; UR, urostyle.

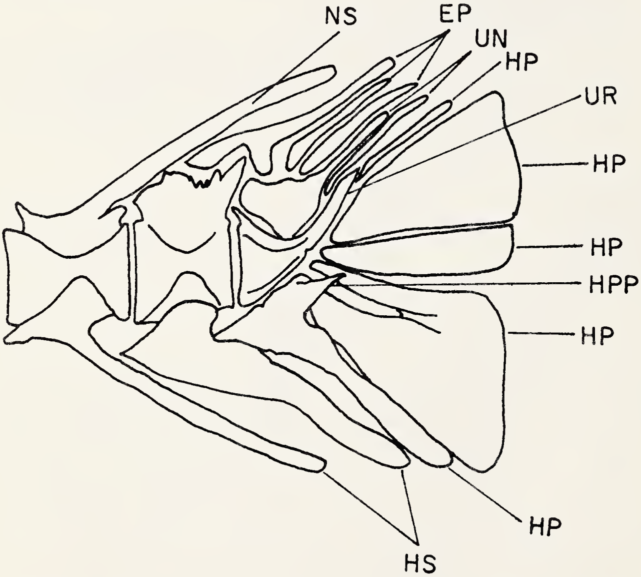

Figure 11. Caudal skeleton of a cleared and stained 32.5 mm juvenile of *N. pectoralis*. Abbreviations as in figure 10.

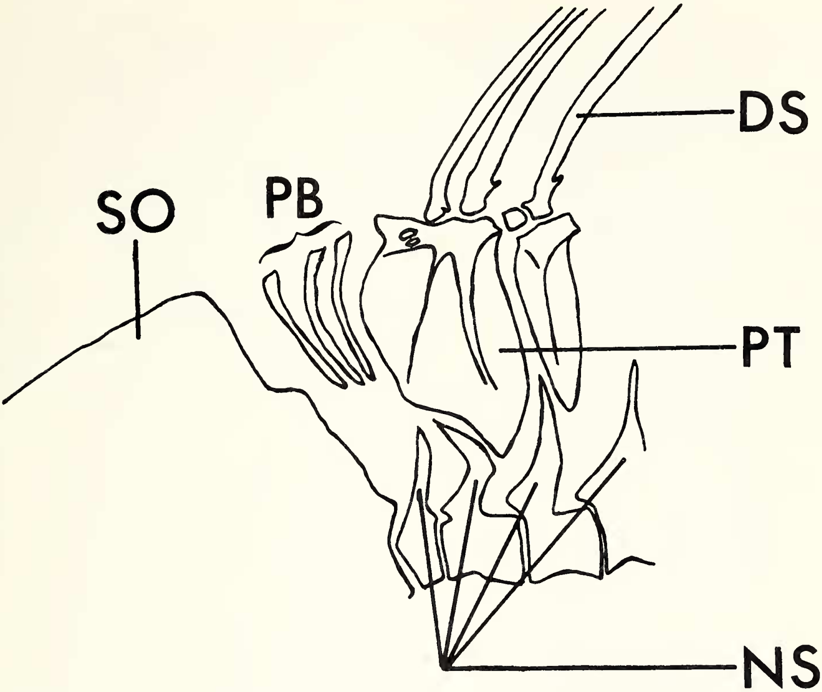

Figure 12. Anterior dorsal fin elements and supporting structures in a 27.5 mm *N. pectoralis*. Abbreviations: DR, dorsay ray; NS, neural spine; PB, predorsal bones; PT, pterygiophore.

fundamentally is not different from that found in carangids, and a moderate expansion of the ventral part of the pterygiophore could carry the first two anal spines away from the third.

CLASSIFICATION AND RELATIONSHIPS

Nematistius differs in several respects from the forms customarily placed in the family Carangidae. For comparative data on the Carangidae we have relied mainly on the important work of Suzuki (1962) and the descriptions of Starks (1911), although we have utilized skeletal and stained and cleared material as well.

The most important difference is the otophysic connection. The adaptive significance of this modification, which would serve to increase both the sensitivity of hearing and the range of frequencies perceived, is obvious. The formation of the otophysic connection has involved important changes in the configuration of the basioccipital and the gas bladder. It is of a type which is, so far as we have been able to determine, unique.

The remaining characters that serve to isolate *Nematistius* from the carangids are less fundamental. There are three normally arranged anal spines, rather than two spines detached from the anal and one at its base. This is not a character of obvious adaptive significance, although it is of great constancy in the Carangidae. The shoulder girdle, though composed of the same elements as in the Carangidae, is different in shape in *Nematistius*. In the Carangidae the coracoid is broad and flattened, and parallel to the cleithrum, from which the lower end sometimes diverges. As a result, the interosseous space (Starks 1930) is much reduced. In *Nematistius* the middle and lower parts of the coracoid are rodlike. The rodlike portion of the coracoid is well separated from the cleithrum, contacting it only ventrally, so that the interosseous space is large.

There is also a difference in the arrangement of the predorsal bones. In *Nematistius* there are two predorsals in advance of the first neural spine and one just behind its tip. In the carangids that we have examined either there is one predorsal before the first neural spine and two before the second, or each of the first three neural spines is preceded by a predorsal bone.

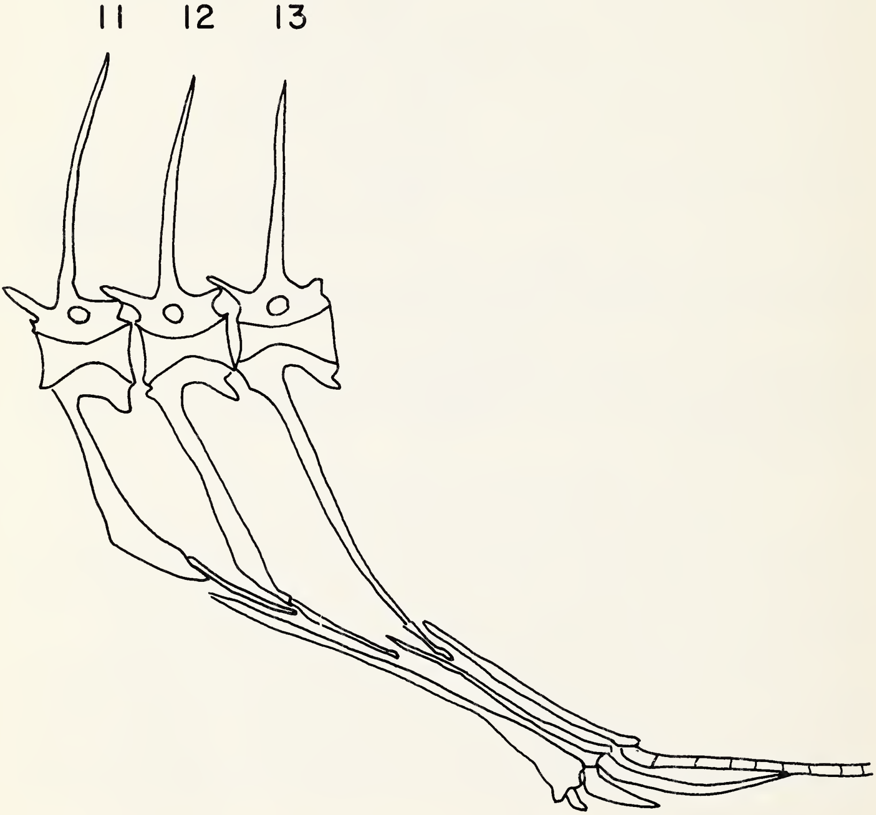

Figure 13. Anterior anal fin elements and associated supporting structures in a 27 mm *N. pectoralis*.

Nematistius also differs from many carangids in that the first pterygiophore is expanded greatly and platelike and bears two spines. The neural spines of the first two centra are crowded and curved forward to accommodate it. We regard this enlarged pterygiophore as the product of fusion of two pterygiophores. This is not in accord with the hypothesis put forward by Smith and Bailey (1961). According to their scheme, in a fish with 3 predorsals and 2 spines on the first proximal pterygiophore (0 -0 -0 -2), the first spine has been displaced backward from the third predorsal bone. However, this does not allow for the derivation of the 0 -0 -0 -2 condition from an ancestor with the 0 -0 -0 -1 condition. And the trends indicated in Smith and Bailey's plate I do not admit such a possibility. However, in the Carangidae both arrangements occur, as well as one not noted by Smith and Bailey, 0 -0 -0 -0 -2 in *Trachinotus*. (It should be noted that the arrangement in *Vomer setapinnis* is 0 -0 -0 -2, not 0 -0 -0 -0 -0 -1 as indicated by Smith and Bailey).

It seems to us that it is simpler to derive the 0 -0 -0 -2 condition from the 0 -0 -0 -1 (especially in the Carangidae, in which the former condition appears to have been derived from the latter several times), by invoking a fusion of two pterygiophores, rather than the moving back of the spine and subsequent or simultaneous loss of the rayless pterygiophore. In *Trachinotus,* however, it is clear that the first spine has migrated backward, because its pterygiophore persists as a fourth predorsal bone. It is likely that studies of the ontogeny of the dorsal fin in carangids will help clarify this admittedly unsettled question.

The 0 -0 -0 -2 condition, however, has been derived independently in *Nematistius* and certain carangid genera, since primitive carangids such as *Seriola* and *Naucrates* have the 0 -0 -0 -1 condition.

We believe that the first three differences discussed above are sufficient to indicate the placement of *Nematistius* in a family distinct from the Carangidae. Nor does the set of features exhibited by *Nematistius* warrant its inclusion in any other fish family. However, the Nematistiidae does agree with the Carangidae in a number of features, and the families are closely related. The similarity in general appearance and in the deeply forked caudal, with the rays clasping the skeletal supporting elements, could be ascribed to convergence. The suite of osteological similarities displayed by the two groups, however, are not so easily explained on this basis.

The neurocranium of a carangid has a very characteristic appearance caused by the strong development of medial and lateral crests. The neurocranium of *Nematistius* is extremely similar to that of certain high-headed, short-snouted carangid genera. Only the tell-tale tunnels on the lateral faces of the basioccipital would allow the separation of a *Nematistius* skull from a group of carangid skulls. Even the peculiar posterior flattening of the parasphenoid of *Nematistius* is paralleled in *Trachinotus*. The circumorbital bones of carangids are likewise distinctive (Suzuki 1962, Figs. 35, 36; Smith and Bailey 1962, plate 3 Q), in that the third suborbital (2SO of Suzuki) bears a broad lamina and articulates with the second mainly along its upper inner edge, rather than posteriorly. The resemblance between the suborbital bones of *Nematistius* and such primitive carangid genera as *Elagatis, Naucrates* and *Seriola* is striking. Another pecularity shared by the two groups is in the structure of the pelvic girdle. In both, the anterior parts of the pelvic bone are thin but broad, with flanges produced ventrally to provide deep grooves for muscle attachment, and the posterior (ischial) processes are elongate and well developed. This characteristic facies can be seen in Suzuki's figures 45A-R, and our figure 9.

The otolith of *Nematistius* resembles that of *Seriola* and *Caranx* in that the rostrum is long and there is a deep notch above it. It further resembles that of *Seriola* in the form of the sulcus (*Caranx* differs somewhat from the other two genera in this respect) and in the serration of the lower margin. The otolith of *Nematistius* is more massive and more crystalline in structure than that of either carangid, but is not very different in either respect (compare figures 14 and 15).

Certain other points of similarity are perhaps of less value, but still serve to emphasize the overall similarity of *Nematistius* to the Carangidae. These include the presence of a well-developed foramen in the ceratohyal and the shape of the hyomandibular, which has a deep groove on its lateral face for the reception of the preopercle.

It is perhaps not surprising that the caudal skeleton of *Nematistius* should resemble that of carangids, considering the similarity of function. Although in most carangids there has been more fusion of elements (compare figures 10 and 11 and figure 16), the caudal skeleton of the primitive but specialized *Trachinotus* (Fig. 17) is like that of *Nematistius* in the retention of three epurals.

The differences between the Nematistiidae and the Carangidae are those of specialization and no feature militates against the derivation of *Nematistius* from a generalized carangid or protocarangid. However, no extant genus qualifies as an ancestor. All of the subfamilies considered primitive by Suzuki are specialized in having two detached anal spines. In the Chorineminae (=Scomberoidinae) the premaxillary is non-protractile, and in the Trachinotinae the supramaxillary has been lost, the pharyngeals are enlarged, and there is a lateral peg on the basioccipital for the attachment of a heavy ligament. Members of the Naucratinae are less specialized, but in addition to the aforementioned difference in arrangement of anal spines, the caudal skeleton of *Seriola* (the only naucratine genus examined osteologically by us) is specialized in fusion and loss of elements present in *Nematistius*.

Freihofer (1963) found that the Carangidae and Nematistiidae differ in the course of the nerves of the ramus lateralis accesorius (RLA), the former having pattern 9 and the latter pattern 10 (reduced). He believed that this means that the Carangidae and Nematistiidae are unrelated and that affinities should be sought among other groups with pattern 10. He stated that "*Nematistius pectoralis* most closely resembles *Medialuna californiensis* which also has pattern 10" and "Cursory examination of the skeletons of *Nematistius* and *Kyphosus* reveals enough general similarities falling within the entire conspectus implied by the Pattern 10 assemblage to leave the hypothesis stand as a good one for future testing."

We have compared the skeleton of *Nematistius* with those of *Medialuna californensis* and *Girella nigricans*. The general similarities indeed are sufficient to indicate an ordinal relationship. Neither form either exhibits or foreshadows the peculiarities of *Nematistius*. Without repeating them, neither are the peculiarities shared by the Nematistiidae and Carangidae found here. Noteworthy differences include the lack of lateral crests on the skull and the restriction of the supraoccipital

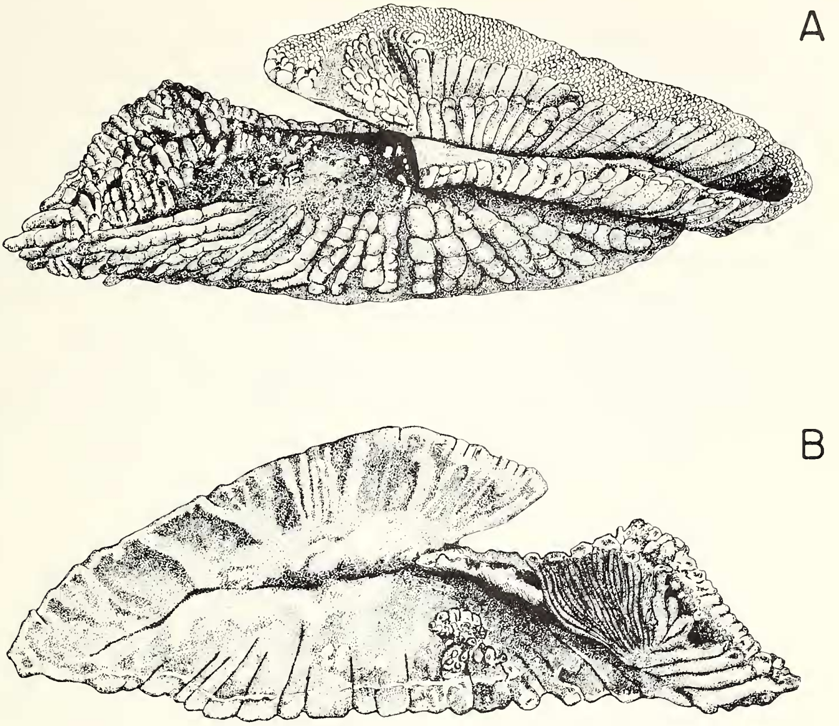

Figure 14. Right sagitta of *N. pectoralis*. A—medial face. B—lateral face.

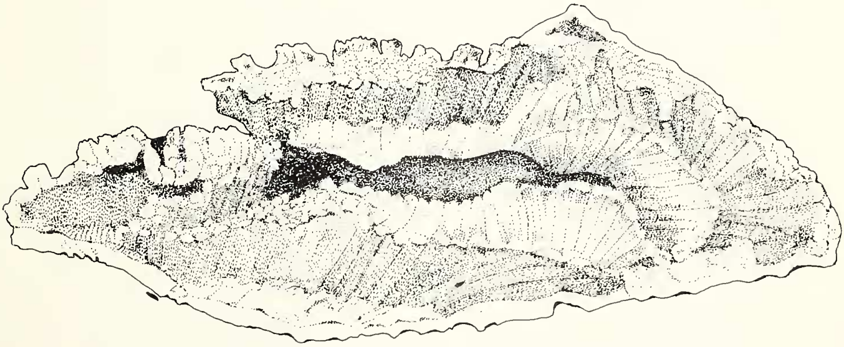

Figure 15. Right sagitta of *Caranx marginatus*, medial face.

crest, which does not encroach on the frontals, which in turn lack a crest. Also the shape of the jaw bones is very different in these nibbling forms. In short, once common perciform characteristics are eliminated, there is little in the osteology of *medialuna* and *Girella* to support the contention that they are especially closely related to *Nematistius*. There is only the evidence of the RLA pattern, and no convincing proof exists that it is the single characteristic by which teleost phylogenies are to be deduced.

Patterson (1964) has argued that the Carangidae (and by extension the Nematistiidae) are not perciform fishes, but that instead they have evolved independently from Beryciformes, and that their perciform characters are due to parallel evolution. This argument was repeated by Greenwood et al (1966:390) and supported by Patterson (1968).

This conclusion is based on a series of similarities between the Cretaceous dinopterygoid beryciform genus *Aipichthys* and certain carangids. Patterson (1964)

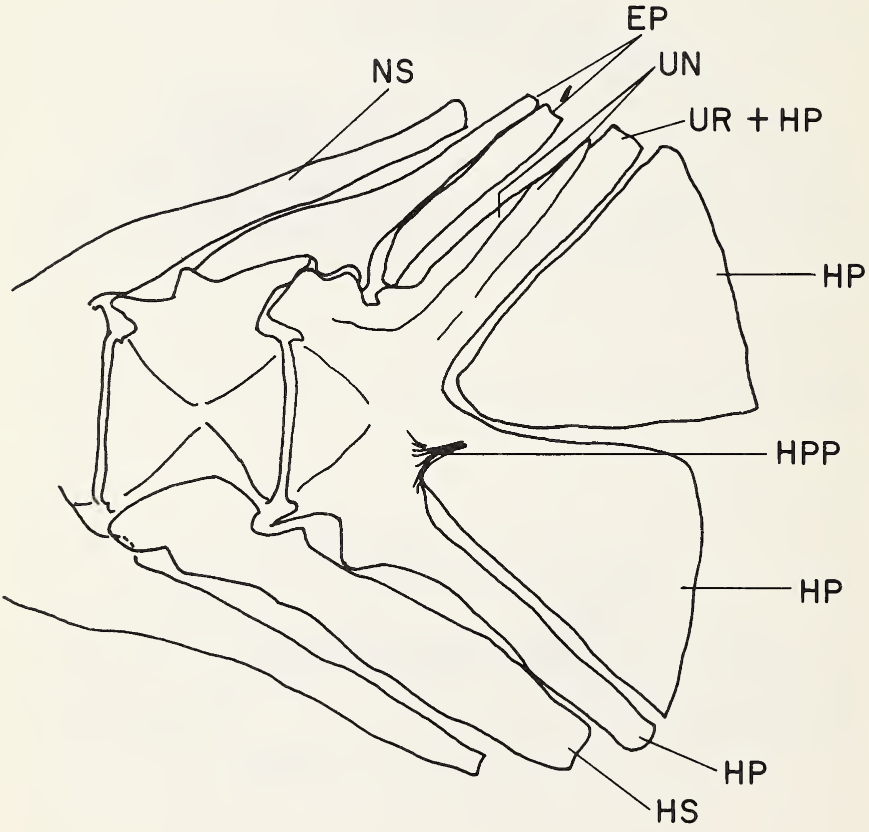

Figure 16. Caudal skeleton of a 50 mm juvenile of *Selene vomer*. Abbreviations as in figure 10.

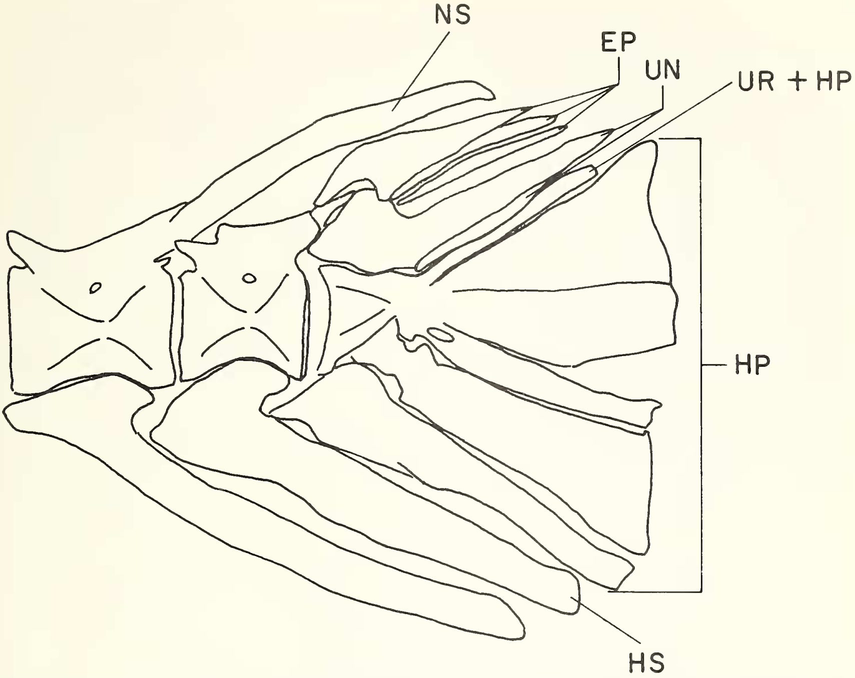

Figure 17. Caudal skeleton of a 73.5 mm juvenile of *Trachinotus glaucus*. Abbreviations as in figure 10.

did not cite the work of Suzuki (1962) or Starks (1911) and figured the osteology of *Vomer,* one of the most specialized and advanced genera of the Carangidae. His concept of the family thus was limited. According to him the chief characters linking *Aipichthys* with the Carangidae are the "deep trunk and long dorsal and anal fins, with few spines and with the anterior soft rays elongated. . . . the high supraoccipital crest. . . . the upturned highly protrusible mouth, the presence of an elongated supramaxilla, the number of vertebrae, the form of the cleithrum and coracoid, the characters of the radials of the dorsal and anal fins, the cycloid scales . . . , and, in particular, the deeply forked bases of the caudal fin-rays" (1964:397). The resemblances between *Aipichthys* and deep-bodied carangids such as *Alectis, Selene, Trachinotus* and *Vomer* were held to be especially close, and "too detailed to be due to convergence alone." The forked caudal rays that clasp the endoskeletal elements also were held to be an important character indicating relationships (1964: 470). Patterson's figure of *Aipichthys* is reproduced for comparison in figure 18.

To begin with, the deep-bodied carangid genera cited by Patterson were regarded by Suzuki (1962) as specialized and (with the exception of *Trachinotus*) advanced. Suzuki regarded the Naucratinae as the most generalized group of carangids and in this we concur. If, as the osteological evidence indicates, *Nematistius* represents an early offshoot from the carangid line, its features must also be accounted for. If phylogeny is to have any meaning, ancestral forms must resemble the generalized representatives of descendant lineages, not the most advanced and specialized ones.

Taking first a similarity utilized by Patterson (1964) that we believe to be more apparent than real, the supraoccipital crest of *Aipichthys* is very different from that of the Carangidae. It apparently stops at the back of the frontals and is not carried forward by them to the ethmoid as it is in carangids and *Nematistius*. A crest such as that of *Aipichthys,* termed the ''chaetodontid type'' by Gosline (1966), can be found in any number of perciforms with short, deep heads. Included would be several genera of embiotocids, *Calamus* (Sparidae), and *Medialuna* (Kyphosidae), certainly an unrelated assemblage. In fact, except that the head is less deep and foreshortened, the crest of *Aipichthys* is not basically different from that of certain polymixioid genera illustrated by Patterson (1964, Figs. 76-78). We concur with Gosline (1966) that it is unlikely that the sharp crest of carangids and *Nematistius* is derived from the broad crest of *Aipichthys*.

The nature of the articulation of the caudal rays to endoskeletal elements is a poor indicator of relationships. Caudal rays with forked bases that wrap around the

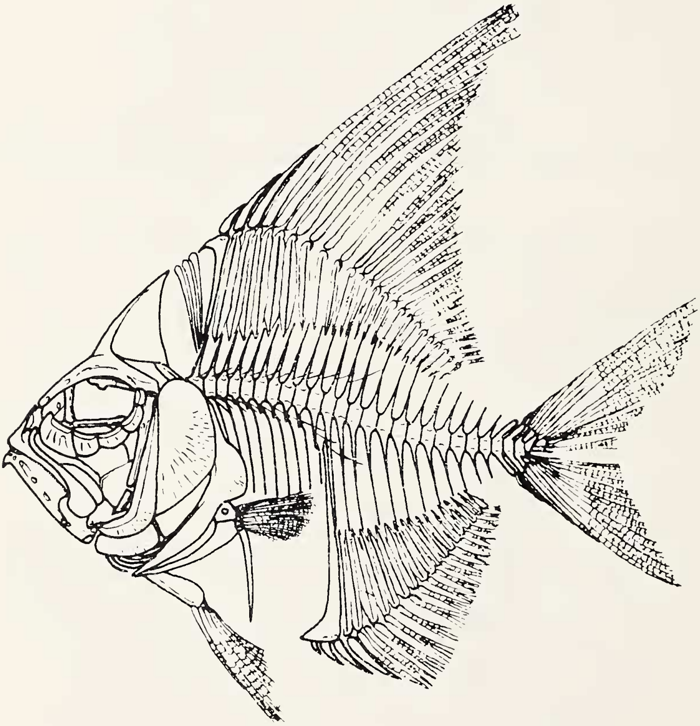

Figure 18. *Aipichthys velifer*. From Patterson, based on Smith Woodward.

tail skeleton are found in fish groups that differ greatly in other respects, and thus must have been evolved independently several times. Such "wrap-around" caudal rays are of course characteristic of the Scombroidei. They are also found in the Echeneiformes, some Atheriniformes (Exocoetoidei), and in the perciform suborder Stromateoidei (Haedrich 1967) (*Peprilus* sp. examined)—a quite unrelated assemblage. Weitzman (1967) has illustrated such rays (although not so dramatically developed) in malacopterygian teleosts such as *Vinciguerria* (Gonostomatidae), *Parasudis* (Paralepididae) and *Saurida* (Synodontidae), and they also occur in the Engraulididae (*Anchoa* examined). The list could be extended, but this should suffice to document our contention.

The upturned, highly protrusible mouth of *Aipichthys* is not a character shared with primitive carangids but with advanced and specialized ones. This sort of mouth, along with a modified suspensorium, appears in certain advanced carangids with scutes along the lateral line, a characteristic absent in *Aipichthys*.

Patterson did not specify the similarities in cleithrum and coracoid, but judging from his figure, the shoulder girdle of *Aipichthys* does not differ from that of most beryciforms, nor, for that matter, from that of generalized perciforms. The coracoid of *Aipichthys* certainly does not resemble the broad, almost straight coracoid of carangids. And, if Patterson's figure is correct, two pectoral actinosts are borne on the coracoid in *Aipichthys*, a character shared neither with the carangids nor most of the Beryciformes.

We are left, then, with a general resemblance in body form between *Aipichthys* and advanced carangids, and the shared characters of elongate and broad dorsal and anal pterygiophores, a low number of vertebrae and cycloid scales.

The superficial resemblances between *Aipichthys* and certain advanced carangids can be ascribed to convergent evolution in fishes with similar ecologies. Certainly the elongation and broadening of the pterygiophores is an obvious adaptation, which serves to stiffen the body in deep-bodied fishes, and is by no means restricted to *Aipichthys* and the Carangidae.

There thus does not seem to be sufficient basis for the removal of the Nematistiidae and the Carangidae from the Perciformes and the postulation of an independent origin of the perciform suite of characters. If the order Perciformes is to be dismembered, the process must begin elsewhere, and on firmer grounds.

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RESUMEN

La posición sistemática del papagallo, *Nematistius pectoralis,* ha estado en duda por largo tiempo. Ha sido considerado alternativamente como miembro de la familia Carangidae o como representante único de una familia monotípica. La investigación de la estructura ósea sugiere, sin embargo, que *N. pectoralis* no debería ser clasificado dentro de la familia Carangidae. *N. pectoralis* difiere de miembros de la familia Carangidae en cuanto a que su vejiga natatoria penetra al cráneo a través de grandes forámenes en los basioccipitales y toma contacto con el oído interno, a que el espacio interoseo de la cintura escapular está bién desarrallado y a que sus tres espinas anales están ubicadas normalmente. Sin embargo, ambas familias son similares en la mayoría de sus otras características óseas y, por lo tanto, se considera que están estrechamente relacionadas.

Se demuestra que la sugerencia de Patterson de que la familia Caragindae habría derivado independientemente de la familia Beryciformis carece de fundamentos: el principal índice de parentesco propuesto por él, rayos caudales con bases ahorquilladas que abrazan las estructuras hipurales, se ha desarrollado independientemente en various linajes no relacionados entre sí. Otras semejanzas entre el género bericoide *Aipichthys* del Cretáceo y carángidos modernos son considerades el producto de la evolución convergente.

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